CERTAIN FEATURES OF SOLENOGASTRE DEVELOPMENT.

BY HAROLD HEATH.

The solenogastres comprise a group of worm-like organisms which for a full half-century have held an unsettled systematic position in zoological literature. Certain features of their organization remind one strongly of the mollusks; others apparently relate them to the worms; and accordingly their classification has depended upon the relative importance given to these resemblances. Numerous works have appeared treating of their anatomy, but up to the present time our knowledge of their development has been confined to two brief papers by Pruvot ('90, '92). The observations therein recorded are so unique in several respects that they have influenced the problem in a negative way only, making it appear that in the development of these organisms we have to deal with matters not closely related to other animals. It has been my good fortune to be able to study a small collection of solenogastre embryos, and I shall endeavor to show that as a matter of fact the development is very clearly molluscan.

In a report on the solenogastres of the North Pacific (Heath, '11), a species, *Halomenia gravida*, was described which carried about twenty-five embryos, in various stages of development, between the branchial folds in the cloacal chamber. These were discovered only after the adult was sectioned, but a careful study of sections and reconstructions has rendered the course of development fairly clear from the one cell stage to the point where the mid-gut, stomodæum, foot and nervous system are distinctly outlined.

At the outset it is well to state that one of the most striking features of solenogastre development is the presence of a vast test, or coat of ciliated cells, which envelops the larva until the metamorphosis, masks the internal structures and so distorts certain details of the development that it may well have appeared to Pruvot and other authors that these animals are unique. I am decidedly of the opinion that Drew ('99) was correct in regarding the test as a modified velum. It is enormous assuredly, but in its relations to other organs and the fact that in several other animals it is shed at the time of the metamorphosis certainly points to more than a superficial resem-

blance. In *Yoldia*, *Teredo* and *Ischnochiton*, for example, the velum is ultimately discarded, and a study of the diagrams (fig. 1) will serve to show that the differences between the development of the solenogastres and the chitons are in large measure due to the size of the test or velum. Whether or not this is a fundamental fact depends upon the history of the early blastomeres, which is lacking at the present time; nevertheless, there are many indications that the two classes of animals have descended from a common ancestor.

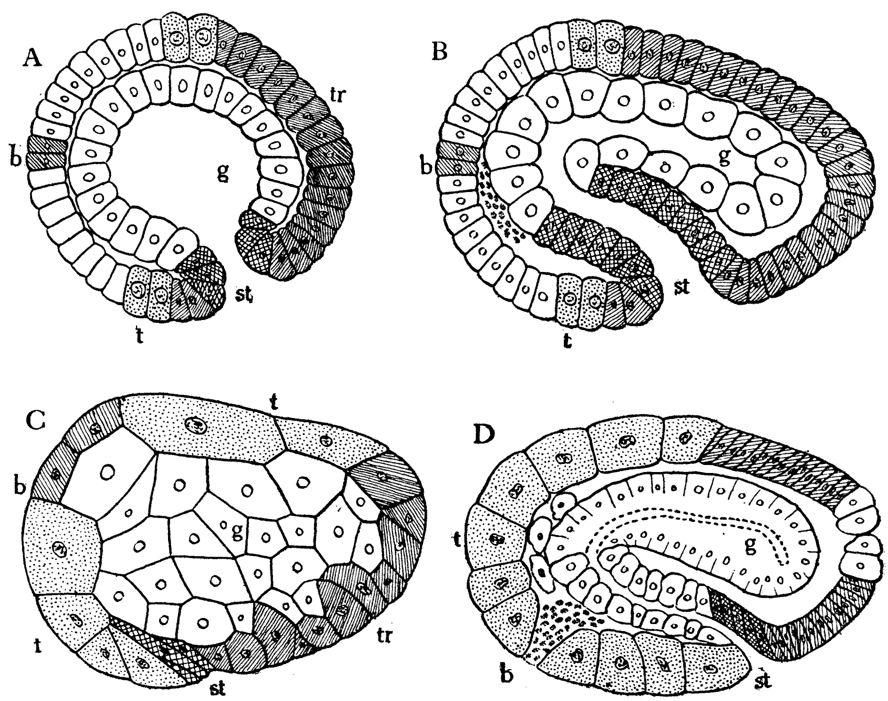

Fig. 1.—Diagrams illustrating the development of the primary germ layers in the chitons (A, B) and solenogastres (C, D). *b*, cells producing the cerebral ganglia; *g*, archenteron; *st*, stomodæum; *t*, test cells. Such devices as stippling, cross-hatching and parallel diagonal lines indicate homologous regions.

The egg of *Halomenia gravida* is a spherical body, densely and uniformly packed with yolk, and is surrounded before it leaves the ovotestis with a distinct vitelline membrane. In the earliest stage represented at least one polar body is distinctly visible, and immediately beneath it the female pronucleus is clearly defined. Close to the equator of the egg another nucleus, probably the male pronucleus, appears with equal distinctness.

In the next stage segmentation has commenced, resulting in 28 cells of approximately equal size. There is no sign of a blastocele or any signs of differentiation. In the succeeding stage fully 100 cells are present and size differences are apparent, but while a slight elongation defines the antero-posterior axis of the larva, the absence of blastocele and stomodæum renders it difficult to accurately define the ventral and dorsal surfaces.

In the following stage the differentiation of the test has commenced and, judging from two larvæ where the polar bodies remain attached, it extends over the greater portion of the dorsal surface and to a considerable extent of the ventral as well (fig. 1, C). The remaining cells, those destined to form the future animal, are thus in large measure enclosed. The cells not included in the test but bordering upon the surface are, generally speaking, of smaller size than those upon the interior (in one specimen this is more marked than in the one figured), but there is up to this time no clear differentiation into ectoderm and endoderm. In the mid-ventral line, in immediate contact with the border of the test, are slender elements (*st*) that represent the first stages in the formation of the stomodæum. The comparatively thin cells (C, *b*) in the neighborhood of the polar body (not represented) are a constant feature and evidently furnish the material for the development of the cerebral ganglia.

In later stages (as in D) the various regions of the body are distinctly outlined, and to some extent the digestive and nervous systems have been sketched in. The stomodæum is clearly differentiated and the mid-gut is outlined, though its constituent cells and cavity are not as yet in an advanced state of development. The cerebral ganglia comprise large masses of cells forming a group anterior to the stomodæum. Posteriorly, these divide, encircle the stomodæum and extend along the ventral surface to the posterior end of the body. At various points in the trunk region between the gut and body wall or test there are a few scattered cells, yolk-laden and accordingly distinguishable from the ganglionic products. They probably are mesoblastic elements.

At the posterior end of the body is a ring of cells, ciliated in *Myzomenia*, that enclose a depressed area bordered in the earliest recognizable stage by relatively slender cells. These last-named elements appear to divide repeatedly and become transformed into a group of cells bordering upon the surface and on the other hand passing without a sharp line of demarcation into the ganglionic cords. In the oldest stage represented the nerve cord appears to be completely

cut off from, though in contact with, a fairly distinct group of cells bordering the surface of the body. It thus appears that the cells enclosed by the ring of larger cells become transformed into a sense organ, perhaps the dorso-terminal sense organ known to occur in many solenogastres.

In the latest stages the test becomes considerably reduced in size and the trunk gains proportionately in prominence. This increase in the extent of the trunk appears to be wholly due to the division of definite ectoderm trunk cells and not to any products supplied by the test. Measurements show conclusively that the test cells gradually shrink in bulk, probably due to the absorption of their nutritive products, and karyokinetic spindles indicate activity on the part of the trunk ectoderm. To what extent this proceeds it is impossible to state. . In early stages there is one, possibly two cells situated immediately beneath the cells (fig. 1, C, *b*) that I believe furnish the material for the cerebral ganglia. In later stages there are indications that this deeper seated cell has undergone a few divisions, and the resulting products occupy the space (fig. 1, D) between the alimentary canal, cerebral ganglia and test cells of the head region. They may possibly represent mesoblastic products, but their relatively large size (for the sake of clearness, they are smaller in the diagram than in reality) and their position suggests that they may supply the material for the head epidermis as the test recedes.

Turning now to the development of the species described by Pruvot, we find that especially in *Proneomenia aglaopheniæ* the early development follows essentially the same path as in *Halomenia*. In the other species, *Myzomenia banyulensis*, there is a decided difference in the size of the cells during the early cleavages, but in both cases the close of segmentation finds the larvæ constructed upon the same plan. The test is evidently of greater size than in *Halomenia* and more completely envelops the remaining cells so that they are hidden in lateral view, but the arrangement of the cells is evidently quite similar to that shown in diagram C. The enclosed elements are supposed to be endodermal in character, and the region (depressed in the species studied by Pruvot) bordered by the test is termed the blastopore. I believe both of these statements are incorrect as I shall now attempt to demonstrate.

Generally speaking, the velum of the trochozoa forms only an insignificant portion of the ectoderm. In the solenogastres it has expanded to such an extent that it comes in contact with the cells destined to form the cerebral ganglia, and posteriorly it forms a

considerable portion of the trunk as well. But the important fact remains that in *Halomenia* the position of the stomodæum, which marks the position of the blastopore, is unmistakable and, as the diagrams show, it is located immediately behind the border of the test on the ventral surface. Furthermore, the diagrams illustrate the fact that there remain many other exposed cells bounded by the test, and these become directly transformed into the trunk ectoderm. In other words, diagram C is a gastrula stage just as certainly as diagram A, the main differences in the solenogastres being correlated with an epibolic type of gastrulation and the enormous size of the velum. The accurate details of the process are lacking and close comparisons are not possible at present, but the important fact is certainly clear that the cells enclosed by the test are not all endoderm and the blastopore is small and typically situated.

In later stages certain developmental processes are described that rest in part upon the assumption that all of the region bounded by the test represents the blastopore. In this depressed area the cells are stated to form, by a species of delamination, the future definitive ectoderm and endoderm. The outer layer, circumscribed by the test, now represents the trunk ectoderm, and in it three invaginations soon appear. One of these remains open and becomes the proctodæum, while the other two soon close and are transformed into mesoblastic bands. Still later the borders of the proctodæum (evidently the large terminal cells of the trunk that form a ring as in D) are said to develop into a sort of caudal button (bouton caudal) that at first projects into the blastocele. Finally the button becomes evaginated and with the trunk ectoderm protrudes beyond the borders of the test.

In commenting upon these observations it is to be noted that a depression exists in *Halomenia* within the terminal ring-like group of large cells, but it is in no way connected with the endoderm. No sign of a proctodæum is evident at this time nor has it put in an appearance in a stage considerably beyond the one represented in diagram D. The caudal button is evidently the group of cells that in *Halomenia* develops from the cells enclosed by the large cells of the terminal ring. As already noted, these at first project into the blastocele, then flatten out, and exposed to the surface are connected with the ventral ganglionic cords. The mesoblast bands are evidently these same cords, as will appear more clearly in connection with the cerebral ganglia.

In the anterior half of the embryo three invaginations now appear

in the test cells on the ventral side. The median one, of a transitory character, is said to represent the stomodæum, but as a stomodæum exists in *Halomenia* in the normal position I am strongly of the opinion that Pruvot is in error regarding this point. The lateral invaginations unite, forming a transverse band, and posteriorly are prolonged to meet the mesoblastic bands of the trunk. Some of the more dorsal elements constitute the cerebral ganglia. In addition, the ectoderm of the head appears to arise wholly from these same lateral invaginations. Such an origin of mesoblast elements is certainly unique, and I have only to state that I believe this entire group is ganglionic. Its posterior union with the ventral cords certainly indicates its nervous character. The anterior enlargements, the future cerebral ganglia, are of unusual size in *Halomenia*, but there is nothing whatever to indicate that they comprise any mesoblastic elements. Furthermore, there is nothing in *Halomenia* to suggest the development of head ectoderm from any of these cells; and the counter theory, that at least in part it may arise from one or two large cells located beneath the cells responsible for the development of the cerebral ganglia, has been noted in a preceding paragraph.[1]

If on the basis of comparative anatomy it is impossible at the present time to definitely place the solenogastres in their proper systematic position, it is obvious that this is more emphatically true where scanty embryological data are the sole criterion. However, it is evident that their development is more in accord with what we find among the mollusks than with any other phylum. The resemblance of the embryo shortly before its metamorphosis is strikingly similar, in several important details, to *Yoldia* or *Dentalium* or to the chitons if we neglect size differences with respect to the test. Plate ('92) has shown that there are good reasons for the belief, long ago expressed by Blainville ('25), that the scaphopods are most closely related to the prosobranchs rather than to the lamellibranchs. The excessively developed tests encountered in certain species of the first- and last-named classes are therefore not of fundamental importance, and furthermore its small size in the chitons is accordingly not a serious obstacle to the theory expressed by several authors that the solenogastres and the chitons are derivatives of a common ancestor. Such a conclusion has been based almost entirely on

[1] A full account of the development of *Halomenia* will appear in connection with a report on the solenogastres from the eastern coast of the United States, but as considerable time must elapse before its completion it has seemed desirable to publish this preliminary account.

anatomical evidence. Whether it will stand the test from the standpoint of embryology can only be decided when our knowledge is more complete.

Literature Cited.

Blainville, D. de. Manuel de Malacologie, 1825.
Drew, G. A. The Anatomy, Habits and Embryology of Yoldia limatula Say. Mem. Biol. Laboratory Johns Hopkins Univ., Vol. 4, No. 3, 1899.
Heath, H. The Solenogastres. Mem. Mus. Comp. Zool. Harvard Univ., Vol. 45, 1911.
Plate, L. Ueber den Bau und die Verwandtschaftsbeziehungen der Solenoconchen. *Zool. Jahrb.*, Abth. f. Anat. u. Ontog., Bd. 5, 1892.
Pruvot, G. Sur le développement d'un Solenogastre. Comp. Rend. Acad. Sci. Paris, Tome III, 1890.
—— Sur l'embryogénie d'une Proneomenia. *Ibid.*, Tome 114, 1892.